
Phylogenetic revision of *Leptodesma* (*Leiopteria*) (Devonian: Bivalvia)

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Abstract

The phylogenetic relationships of Middle and Late Devonian species of the subgenus *Leptodesma* (*Leiopteria*) Hall 1883 are examined cladistically and a taxonomic revision of the subgenus is proposed. Six taxa previously afforded species rank are synonymized with *Leptodesma* (*Leiopteria*) *laevis* (Hall 1843). One new species, *Leptodesma* (*Leiopteria*) *accranus*, is described from the Lower to Middle Devonian of Ghana. Biogeographic analysis of the subgenus reveals less vicariant speciation than speciation associated with range expansion and dispersal. This pattern has been observed in trilobites and phyllocarid crustaceans and may represent a general pattern during the Middle and Late Devonian. Extensive range expansion may have played a role in governing biodiversity dynamics before and during the Late Devonian biodiversity crisis.

Keywords

Phylogeny, biogeography, Devonian, North America, pterinoid, bivalve, speciation, extinction.

Abbreviations

AMNH	American Museum of Natural History
MPM	Milwaukee Public Museum
NYSM	New York State Museum
PRI	Paleontological Research Institution
USNM	Smithsonian Institution
UMMP	University of Michigan Museum of Paleontology
YPM	Yale Peabody Museum

Introduction

Leptodesma (*Leiopteria*) Hall 1883 is a species-rich and cosmopolitan subgenus that occurs from the Middle Silurian through the Permian. Its maximal diversity was during the Middle and Late Devonian and the number of species de-

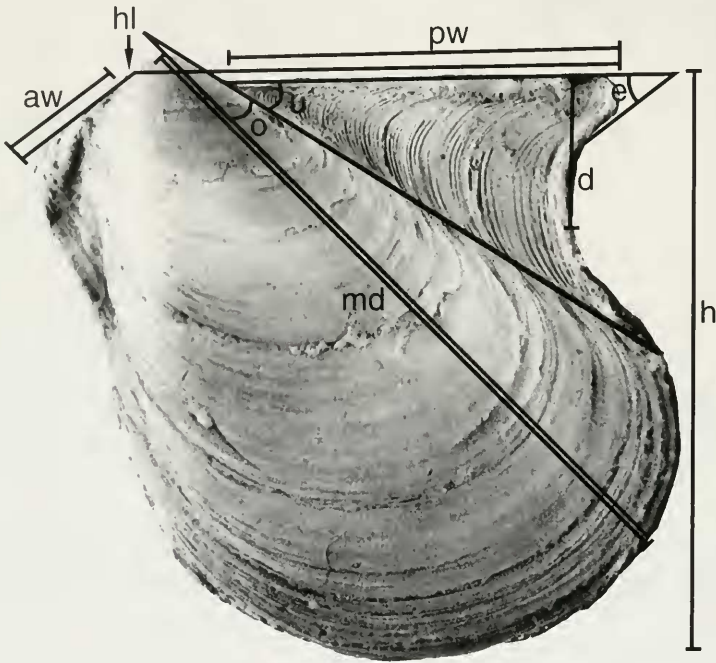


Figure 1

Location of morphological measurements illustrated on *Leptodesma (Leiopteria) ausablensis* (UMMP 38114). *Abbreviations:* aw, length of anterior wing; d, distance from hingeline to inflection of posterior embayment; e, angle of posterior wing extension; h, shell height measured perpendicular to hingeline; hl, length of hingeline; md, maximum shell dimension or greatest oblique length; o, angle of obliquity; pw, length of posterior wing; u, posterior umbonal angle.

scribed from strata of this age exceeds the total subsequent late Paleozoic diversity of the subgenus. While several studies have revised aspects of its taxonomy (for example, Ehlers and Wright 1959; McAlester 1962), no comprehensive taxonomic revision of Devonian *Leptodesma (Leiopteria)* has been undertaken previously. This paper presents a phylogenetic analysis of Middle and Late Devonian *Leptodesma (Leiopteria)*, primarily from North America, to assess species validity, taxonomy,

and evolution of this subgenus.

Although Hall (1883) assigned species to *L. (Leiopteria)* in his *Paleontology of New York*, a detailed diagnosis of the genus was published in the *First Annual Report of the New York State Geologist*, and included bivalves with oblique, aviculoid shells, an auriculate anterior extremity, a large posterior wing, and a lack of radial ornament (Hall 1884a). This description was later revised by Spriesterbach (in Spriesterbach and Fuchs 1909) to include

details of the musculature and hinge teeth, morphological features not observable on Hall's specimens. Spriesterbach also rejected the inclusion of many European species previously placed within *L. (Leiopteria)* by Frech (1891) and other authors, and supported assignment of those species to other pteroid genera. Williams and Breger (1916) provided a comprehensive review of the status of the genus and included North American and European species.

Newell and La Rocque (1969) revised the taxonomic position of *L. (Leiopteria)* by placing it as a subgenus within the genus *Leptodesma*, as the sister to *L. (Leptodesma)*. The primary distinguishing feature between the subgenera was considered to be whether the anterior auricle was rounded, as in *L. (Leiopteria)*, or acuminate, as in *L. (Leptodesma)*. Recent analyses by Pojeta and others (1986), Bradshaw (1999), and Boyd and Newell (2001) have continued the subgeneric designation of *L. (Leiopteria)* as a valid taxon, and it is used that way in this paper. McAlester (1962) published a comprehensive revision of the Chemung bivalves of New York State and expressed doubts about the validity of Hall's (1883, 1884a, 1884b) species of *L. (Leiopteria)*. McAlester (1962) suggested that many of the Middle Devonian species were merely subjective synonyms, a result confirmed to some extent here.

This paper presents the first phylogenetic revision of *L. (Leiopteria)*, although various authors have indicated the need for such a revision (McAlester 1962; Pojeta and others 1986; Boyd and Newell 2001). The phylogeny derived here is also used to examine biogeographic patterns

of North American *L. (Leiopteria)* during the Middle and Late Devonian.

Phylogenetic Analysis

Taxa analyzed

Specimens representing 22 Devonian species of *Leptodesma*, mostly *L. (Leiopteria)*, were analyzed. All species known from the Middle and Upper Devonian and several Lower Devonian species from North America (those for which sufficient morphological information exists) were included in the phylogenetic analysis. Because the focus of the analysis was determination of evolutionary and biogeographic patterns during the Middle and Upper Devonian, most species of *L. (Leiopteria)* from older and younger strata were excluded. *L. (Leiopteria) marylandica* Clarke and Schwartz 1913 was removed from the analysis due to lack of character information for many character states. *Leptodesma (Leptodesma) spinerigum* (Conrad 1842) was used as the outgroup for character polarization. This taxon was chosen because it is a well-characterized member of *L. (Leptodesma)*, the presumed sister taxon to *L. (Leiopteria)*.

Specimens from the collections of the American Museum of Natural History, Milwaukee Public Museum, New York State Museum, Paleontological Research Institution, Smithsonian Institution, University of Michigan Museum of Paleontology and Yale Peabody Museum were examined.

Characters and character states

Parsimony analysis was conducted using 27 external characters (see Table 1). Although internal characters, such as muscle

Table 1

Characters and character states used in the phylogenetic analysis; (0) represents the presumed primitive state. Morphological terminology follows Cox and others (1969) and Boyd and Newell (2001). Location of morphological measurements are illustrated in Figure 1.

General characters:

1. Angle between hingeline and line of demarcation separating posterior wing from body: (0) small ($\leq 26^\circ$); (1) large ($\geq 29^\circ$). This is comparable to the posterior umbonal angle of Rau (1955).
2. Angle between edge of posterior wing and axis of greatest length (obliquity): (0) small ($\leq 16^\circ$); (1) large ($\geq 18^\circ$). This is comparable to the median umbonal angle of Rau (1955).
3. Overall shape: (0) rectangular, length much longer than width; (1) square, length and width subequal.
4. Size of individual (height perpendicular to hingeline): (0) small (≤ 23 mm); (1) medium (25 to 38 mm); (2) large (≥ 42 mm).
5. Relative size of hingeline (length of hingeline/greatest oblique length, measured from beak to posteroventral margin of shell): (0) long (≥ 0.78); (1) short (≤ 0.72).
6. Location of maximum valve width: (0) hingeline; (1) lateral to hingeline.
7. Convexity of left valve (umbonal height/umbonal width): (0) high (≥ 0.25); (1) low (≤ 0.20).
8. Relative height of umbo: (0) greatly extended above main shell (as in Figure 6.3); (1) moderately extended above main shell (as in Figure 5.5).

Anterior features:

9. Shape of auricle: (0) acuminate; (1) rounded.
10. Form of auricle: (0) extended into point; (1) truncated.
11. Relative size of anterior auricle (anterior auricle width/width of entire hingeline): (0) small (≤ 0.19); (1) large (≥ 0.21).
12. Septum separating auricle from rest of shell: (0) absent; (1) present.
13. Development of byssal sinus: (0) weakly impressed; (1) deeply impressed.
14. Curve of anterior margin: (0) smooth; (1) undulating.

Posterior features:

15. Relative size of posterior wing (posterior wing width/width of entire hingeline): (0) large (≥ 0.63); (1) small (≤ 0.60).
16. Embayment of posterior wing: (0) pronounced; (1) weak.
17. Position of inflection on posterior margin (distance to inflection/valve height): (0) proximal (≤ 0.20); (1) distal (≥ 0.23).
18. Angle of posterior wing extension, measured from hingeline to lateral margin of posterior wing at the extremity: (0) small ($\leq 45^\circ$) (as in Figure 5.6); (1) large ($\geq 50^\circ$) (as in Figure 5.2).
19. Separation of posterior wing from body: (0) demarcated by distinct narrow groove; (1) weakly defined.

Continued.

Table 1 continued

Characters of the comarginal ornamentation:

20. Development of concentric growth lamellae: (0) constant over shell; (1) more strongly developed on posterior portion of shell.
21. Width of growth lamellae: (0) all of equal width; (1) width increases posteriorly.
22. Relief of growth lamellae: (0) low; (1) prominent.
23. Sharpness of growth lamellae: (0) dull; (1) sharp.
24. Growth lamellae: (0) single, distinct rows; (1) lamellose bands; (2) crenulated.
25. Spacing of growth lamellae: (0) irregular; (1) regular.
26. Distribution of growth lamellae: (0) ungrouped; (1) grouped.
27. Radial ornament: (0) absent; (1) weakly developed on right valve; (2) weakly developed on both valves; (3) weakly developed on left valve.

scars, are occasionally useful in species level taxonomy of this group (see Bradshaw 1999), such character information is only available for a handful of studied species. Location of morphological measurements are illustrated in Figure 1; see Table 2 for character coding of analyzed taxa.

Parsimony analysis

Phylogenetic analysis used PAUP* v. 4.0b10 (Swofford 2002). The data set was subjected to a heuristic search using a random addition sequence with 1000 random replications, with tree-bisection-reconnection as the branch swapping algorithm. Taxa containing multiple states for a character were treated as polymorphic for that state. All islands found within the analysis were exhaustively examined, suggesting that additional islands may not exist. All characters were treated as unordered. Characters were optimized with the accelerated transformation (ACCTRAN) option.

Thirteen most-parsimonious trees with a length of 119 steps were recovered.

The strict consensus tree is presented in Figure 2. The consistency index is 0.49 for these trees, and the retention index is 0.56. This observed consistency index exceeds those derived from sets of similarly sized matrices constructed from random data (consistency index of 0.16) at the 0.05 level of significance (Klassen and others 1991).

The phylogenetic analysis was also performed following removal of the species synonymized with *L. (Leiopteria) laevis* (see "Systematic Paleontology" below). The character coding for the revised *L. (Leiopteria) laevis* analysis was taken from the character optimization of the node at the base of the *L. (Leiopteria) laevis* clade from the first analysis, using MacClade v. 3.04 (Maddison and Maddison 1992). Using the PAUP* branch and bound algorithm, two most-parsimonious trees were recovered. The strict consensus tree is presented in Figure 3. The tree length is 83 steps, consistency index is 0.470, and retention index is 0.488. The consistency index exceeds consistency indices constructed from random data of

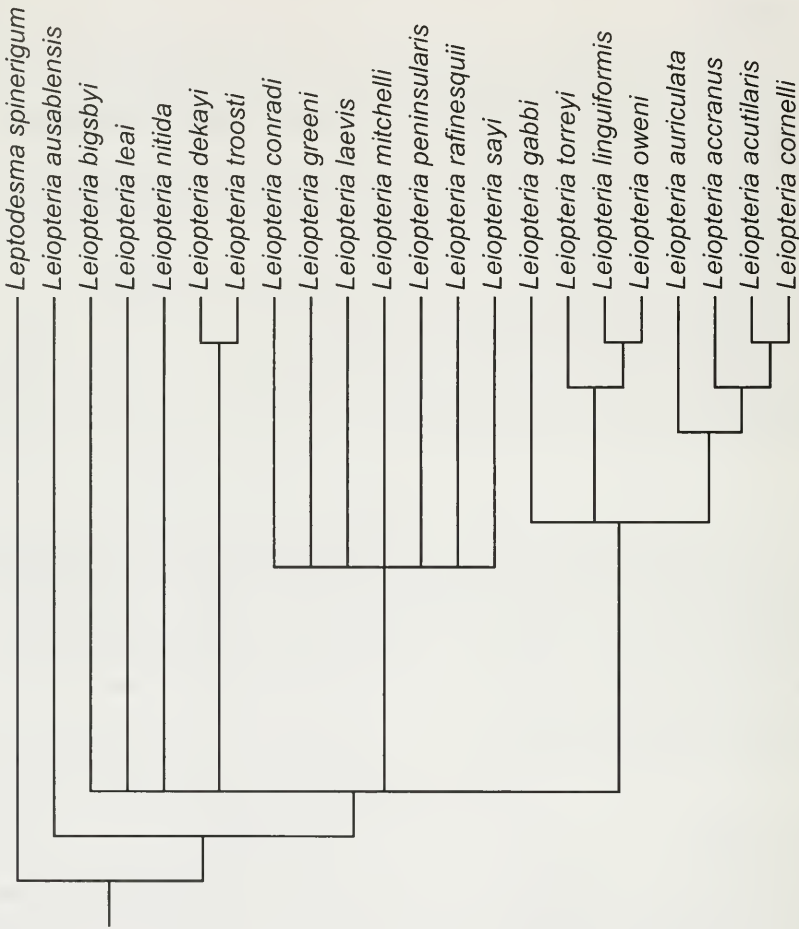


Figure 2

Strict consensus of 13 most-parsimonious trees produced from analysis of character data in Table 1, using PAUP* v. 4.0b10 (Swofford 2002). Tree length is 119 steps. Note the agreement of all trees on the monophyly of the *L. (Leiopteria) laevis* clade.

similarly sized matrices (consistency index of 0.27) at the 0.05 level of significance (Klassen and others 1991).

Support for specific nodes within the recovered cladogram was characterized using jackknife analysis to provide information about the stability of the position of branches when a portion of the charac-

ter data is eliminated (Felsenstein 1985; Sanderson 1989). The jackknife analysis was performed using a full heuristic search with 1000 replicates. Groups compatible with the 50% majority rule consensus tree were retained. The confidence values for the nodes duplicated in the jackknife analysis are presented in

Figure 3. The jackknife values show strong support for the cladogram recovered in the revised analysis, as all branches were replicated in the jackknife analysis with a high frequency.

Further support for the cladogram was found using the g_1 statistic, a measure of the skewness of tree length distributions and phylogenetic signal (Hillis 1991; Hillis and Huelsenbeck 1992). The g_1 value from a distribution of 100,000 trees constructed from this data set is -0.216 , markedly stronger than in random data and significant at the $p = 0.05$ level (Hillis and Huelsenbeck 1992), indicating considerable phylogenetic structure within the data.

Results and Taxonomic Implications

Recognition of clades within subgenus

Since the reanalysis of the data using the synonymy of *L. (Leiopteria) laevis* produced greater topological resolution with excellent support, the discussion below centers primarily on the results presented in Figure 3.

Several patterns are apparent from inspection of the strict consensus cladograms in Figures 2 and 3. First, *L. (Leiopteria) ausablensis* Ehlers and Wright 1959 consistently occupies a basal position while the remaining ingroup species form a well-resolved monophyletic assemblage. Second, three well-resolved groups occur among the other *L. (Leiopteria)* species: (1) a clade composed of *L. (Leiopteria) leai* Hall 1884b, *L. (Leiopteria) dekayi* Hall 1883, and *L. (Leiopteria) troosti* Hall 1884b; (2) a clade of *L. (Leiopteria) nitida* Hall 1883 and *L. (Leiopteria) laevis* (Hall 1843) (which includes the formerly described

species *L. [Leiopteria] laevis*, *L. [Leiopteria] conradi* Hall 1883, *L. [Leiopteria] greenii* Hall 1883, *L. [Leiopteria] mitchelli* Hall 1883, *L. [Leiopteria] peninsularis* La Rocque 1950, *L. [Leiopteria] rafinesquii* Hall 1883, and *L. [Leiopteria] sayi* Hall 1884b); and (3) a clade comprising *L. (Leiopteria) torreyi* Hall 1884b, *L. (Leiopteria) linguiformis* Hall 1884b, *L. (Leiopteria) oweni* Hall 1883, *L. (Leiopteria) gabbi* Hall 1884b, *L. (Leiopteria) auriculata* Clarke and Schwartz 1913, *L. (Leiopteria) accranus* n. sp., *L. (Leiopteria) acutularis* Pohl 1929, and *L. (Leiopteria) cornelli* Caster 1930. Additionally, the relationship of *L. (Leiopteria) bigsbyi* to other subclades is uncertain.

Each of these clades is supported by specific character evidence. The monophyly of all species of *Leiopteria* is supported by the rounded and truncated shape of the anterior auricle (characters 9 and 10). *L. (Leiopteria)* species exclusive of *L. (Leiopteria) ausablensis* share several additional synapomorphies, including an enlarged angle between the hingeline and the line of demarcation separating the posterior wing from the body (posterior umbonal angle), shell of medium size (25 to 38 mm), a deeply impressed byssal sinus, and regularly distributed growth rings (characters 1, 4, 18 and 25).

The first major clade supported by the parsimony analysis includes *L. (Leiopteria) laevis*, *L. (Leiopteria) mitchelli*, *L. (Leiopteria) rafinesquii*, *L. (Leiopteria) conradi*, *L. (Leiopteria) greenii*, and *L. (Leiopteria) sayi* and *L. (Leiopteria) peninsularis* (Figure 5.4, 5.5 and 5.6). The strict consensus tree (Figure 2) shows the monophyly of this group, but does not provide resolution within the clade. Due to the instability of this group and the

Table 2

Character state distribution for taxa in the phylogenetic analysis. Missing data indicated by "?". Character states listed as X, Y and Z are polymorphic, where X=(0&1), Y=(1&2), and Z=(2&3). Character numbers are listed across the top.

	123456789	1111111111	22222222
		0123456789	01234567
<i>L. (Leiopteria) accranus</i>	111000?11	1110111011	00110110
<i>L. (Leiopteria) acutilaris</i>	110011001	111111?1?0	00112100
<i>L. (Leiopteria) auriculata</i>	110000001	1110111111	11000000
<i>L. (Leiopteria) ausablensis</i>	010000001	1010100001	10000002
<i>L. (Leiopteria) bigsbyi</i>	11X10X001	10XXX0101X	00100100
<i>L. (Leiopteria) conradi</i>	11110X1X1	101110X10X	01X11110
<i>L. (Leiopteria) cornelli</i>	010001001	1000101111	00110100
<i>L. (Leiopteria) dekayi</i>	100101001	1010000?00	01110100
<i>L. (Leiopteria) gabbi</i>	110000001	10100111?0	00001110
<i>L. (Leiopteria) greeni</i>	111000101	101000011X	01X11110
<i>L. (Leiopteria) laevis</i>	1111001X1	1111110010	00010XXY
<i>L. (Leiopteria) leai</i>	11X100001	1110100000	00100100
<i>L. (Leiopteria) linguiformis</i>	110211011	1110000110	10001100
<i>L. (Leiopteria) mitchelli</i>	111200101	1011?0X010	01011110
<i>L. (Leiopteria) nitida</i>	11X100001	101XX00010	00010100
<i>L. (Leiopteria) oweni</i>	010211?11	1000?000?1	00001112
<i>L. (Leiopteria) peninsularis</i>	111100101	1011110000	01011110
<i>L. (Leiopteria) rafinesquii</i>	10X100101	101XX00000	010X1X10
<i>L. (Leiopteria) sayi</i>	111100111	1010000101	00001110
<i>L. (Leiopteria) torreyi</i>	110010011	1010001110	00000100
<i>L. (Leiopteria) troosti</i>	100111001	1?10001000	1011210Z
<i>L. (Leptodesma) spinerigum</i>	000000000	0000000000	00000003

relative lack of characters that unambiguously define species, I synonymize these aforementioned six species with *L.*

(*Leiopteria*) *laevis* (see "Systematic Paleontology" below). The synonymy of many of Hall's species has been previously supported by McAlester (1962). The monophyly of the revised *L. (Leiopteria) laevis* is supported unambiguously by reduced convexity of the shell (character 7). The revised strict consensus tree (Figure 3)

places *L. (Leiopteria) nitida* as the sister taxon to *L. (Leiopteria) laevis*, and is supported by the shared development of sharp growth rings (character 23) (Figure 5.3, 5.4, 5.5 and 5.6).

The clade of *L. (Leiopteria) leai*, *L. (Leiopteria) dekayi* and *L. (Leiopteria) troosti* is supported by a sharp angle of posterior wing extension and prominent growth ring relief (characters 18 and 22) (Figure 6.1 and 6.2). Within this clade, the

sister relationship of *L. (Leiopteria) dekayi* and *L. (Leiopteria) troosti* is supported by all most-parsimonious reconstructions (Figures 2 and 3) as well as by jackknife analysis (Figure 3). These two species share the synapomorphies of a small angle between the edge of the posterior wing to the axis of greatest length (median umbonal angle), the widest dimension of the shell located lateral to the hingeline, and sharp concentric growth rings (characters 2, 6 and 23) (Figure 6.2).

The third clade supported by all most-parsimonious reconstructions includes the species *L. (Leiopteria) torreyi*, *L. (Leiopteria) linguiformis*, *L. (Leiopteria) oweni*, *L. (Leiopteria) gabbi*, *L. (Leiopteria) auriculata*, *L. (Leiopteria) accranus*, *L. (Leiopteria) acutularis* and *L. (Leiopteria) cornelli*. The monophyly of this clade is supported by a decrease in size from moderate to small and the movement of the posterior wing inflection from a proximal to distal position (characters 4 and 17) (Figure 6.3, 6.4, 6.5 and 6.6). Within this group there are two smaller clades. The first of these includes *L. (Leiopteria) linguiformis* and *L. (Leiopteria) oweni* as sister taxa, with *L. (Leiopteria) torreyi* as the sister species of that group. The sister group relationship of *L. (Leiopteria) linguiformis* and *L. (Leiopteria) oweni* is supported by three characters: their large size, maximal shell width lateral to the hingeline, and lamellose comarginal ornamentation (characters 4, 6 and 24). The relationship of *L. (Leiopteria) torreyi* to these species is supported by the synapomorphies of a reduced hingeline and umbo (characters 5 and 8) (Figure 6.3). The second clade within this species group includes *L. (Leiopteria) gabbi*, *L.*

(Leiopteria) auriculata, *L. (Leiopteria) accranus*, *L. (Leiopteria) acutularis* and *L. (Leiopteria) cornelli*. This grouping is supported by a synapomorphous enlarged posterior wing (character 15). The monophyly of the remainder of the group exclusive of *L. (Leiopteria) gabbi* is supported by the development of a large anterior auricle and a strong separation of the posterior wing (characters 11 and 19) (Figure 6.4, 6.5 and 6.6). The monophyly of *L. (Leiopteria) accranus*, *L. (Leiopteria) acutularis* and *L. (Leiopteria) cornelli* is supported by growth lamellae, which are both sharp and prominent (characters 22 and 23), and the sister relationship of *L. (Leiopteria) acutularis* and *L. (Leiopteria) cornelli* is supported by the maximal width of the valve developed lateral to the hingeline (character 6).

Evolutionary and ecological implications

Apparently, many of the features reflecting evolutionary changes and speciation within *L. (Leiopteria)* involve aspects of the overall shape and size of species, as well as the development of features of the anterior and posterior wings. Ornamentation changes do not appear to be as important. The relative development of the anterior and posterior wings may be related to the paleoecology of different species. In general, *Leptodesma* and similar members of the Pterineidae have been interpreted as endobysate to epibysate, or epiphytic–epizoic (Kauffman 1969; Pojeta 1971; Stanley 1972; Johnston 1993; Bradshaw 1999). The arguments favoring these different modes of life center on comparisons with modern pterineids, wear pattern of comarginal ornamentation, and inferred musculature (see John-

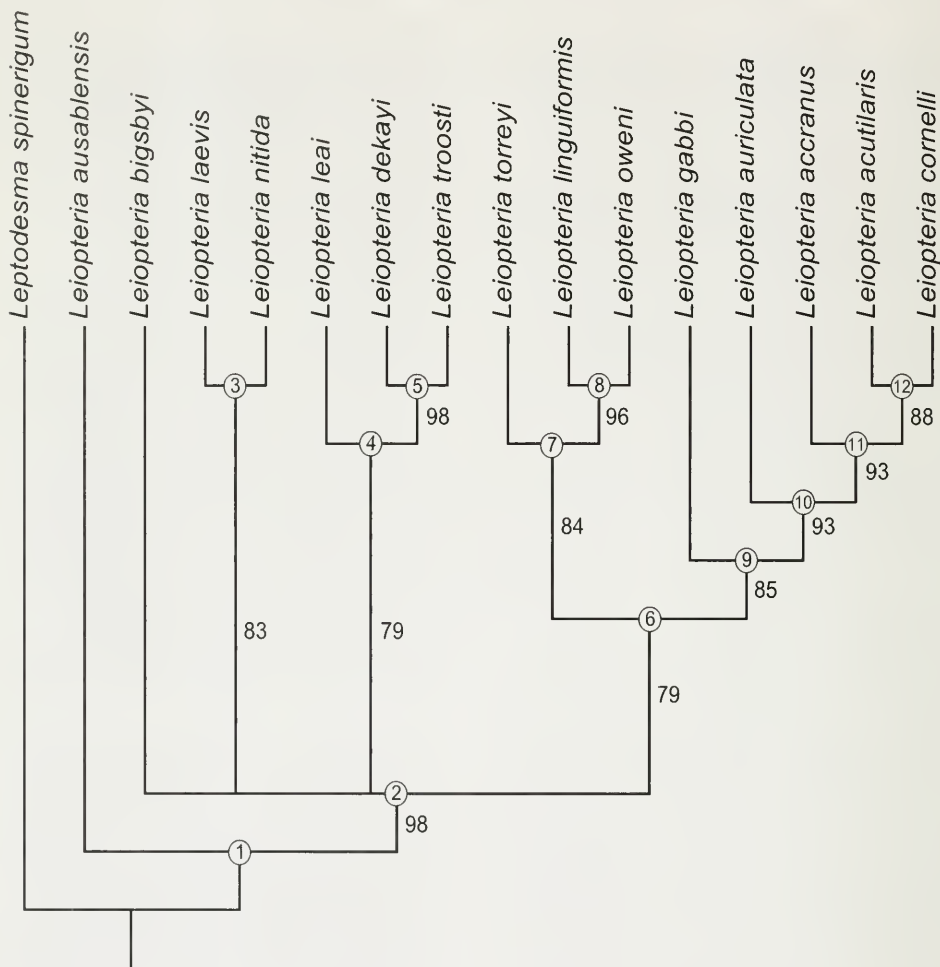


Figure 3

Strict consensus of two most-parsimonious trees produced from analysis of character data in Table 1 with PAUP* v. 4.0b10 (Swofford 2002) when the *L. (Leiopteria) laevis* is considered as a single species following the synonymy proposed in the text. Tree length is 83 steps; retention index is 0.49; consistency index is 0.47; g_i statistic for tree is -0.216 . Jackknife values are indicated next to the node that they support. Character states were placed at the nodes using MacClade v. 3.04 (Maddison and Maddison 1992) under ACCTRAN optimization. Node numbers are circled on the cladogram. Apomorphic characters that change unambiguously below a node are listed in parentheses. Node 1, 9(1); 10(1); Node 2, 1(1), 4(1), 18(1), 25(1); Node 3, 23(1); Node 4, 18(0), 22(1); Node 5, 2(0), 6(1), 23(1); Node 6, 4(0), 17(1); Node 7, 5(1), 8(1); Node 8, 4(2), 6(1), 24(1); Node 9, 15(1); Node 10, 11(1), 19(1); Node 11, 22(1), 23(1); and Node 12, 6(1).

ston 1993 for a detailed review). It is possible that some synapomorphies of clades recovered in this analysis, such as relative wing size or embayment development, may have allowed the included species to inhabit slightly different environments, or inhabit similar environments in slightly different ways.

The possible link of clade differentiation to paleoenvironment is apparent in the first two clades discussed above. All species within the *L. (Leiopteria) leai*, *L. (Leiopteria) dekeyi* and *L. (Leiopteria) troosti* clade are found preserved in a siltstone to sandstone matrix. This may indicate that this clade radiated and was subsequently confined to a high energy shallow marine environment. On the other hand, all specimens of the revised *L. (Leiopteria) laevis* were collected from a matrix of dark shale to siltstone or fine-grained limestone, which may indicate a deeper water or lower energy environmental preference, or both. However, the third clade, which includes *L. (Leiopteria) gabbi*, does not have a definite pattern of lithologic association (presumed environmental preference), as included species are patchily found in sandy, silty, and muddy lithologies.

Another pattern apparent from Figure 3 concerns the stratigraphic ranges of the species and their positions on the cladogram. Neither of the first two clades (*L. (Leiopteria) dekeyi* and the others of this group, or *L. (Leiopteria) laevis* and *L. (Leiopteria) nitida*) have member species that range beyond the Frasnian. The third clade (*L. (Leiopteria) gabbi* and others), however, includes both a Famennian and Mississippian species (*L. (Leiopteria) linguiformis* and *L. (Leiopteria) cornelli*,

respectively). Therefore, this could be the only clade of *L. (Leiopteria)* species that survived the Late Devonian biodiversity crisis and may have been the ancestral stock for the Mississippian and younger species of *L. (Leiopteria)*. To further address this issue, studies including additional Mississippian taxa would be desirable.

Paleobiogeographic Analysis

Methods

Paleobiogeographic patterns in *L. (Leiopteria)* were evaluated in conjunction with the phylogeny presented in Figure 3. This involved first substituting species' geographic distributions for species' names. Geographic distributions were assigned to presumed areas of endemism that existed in the Devonian. Large-scale geological features define the boundaries of these areas of endemism, supported by the presence of large numbers of unique taxa across the entire fauna in each of the regions. The areas of endemism considered within this analysis were: the Northern Appalachian Basin, which includes the Devonian strata in modern New York; the southern Appalachian Basin, which includes Devonian strata in modern southern Pennsylvania, Maryland and Virginia; the Michigan Basin, which includes Devonian strata in modern Michigan, western Ohio and southwestern Ontario; central North America, which includes Devonian strata in modern Wisconsin and Missouri; western North America, which includes Devonian strata in modern Nevada; and West Africa, which includes Devonian strata in modern Ghana. Cer-

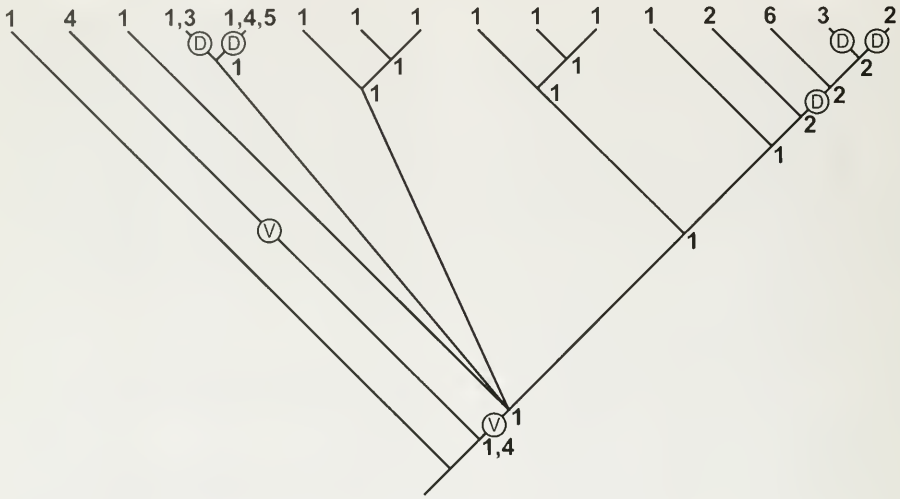


Figure 4

Phylogeny from Figure 2, with biogeographic states substituted for terminal taxa and mapped onto the ancestral nodes. Inferred episodes of speciation by vicariance (V) and dispersal (D) are indicated. Ancestral nodes calculated using a modified Fitch optimization (Lieberman and Eldredge 1996; Lieberman 2000). 1, Northern Appalachian Basin; 2, Southern Appalachian Basin; 3, Mid-continent; 4, Michigan Basin; 5, Western North America; 6, Northern Africa.

tainly, other areas of endemism existed, but Devonian *L. (Leiopteria)* species were either not present in those regions or could not be obtained from them for study. In addition, although some of these regions could potentially be more finely divided biogeographically, this would create several additional regions with only a single taxon. This was not pursued because areas with only a single taxon can lead to artifactual problems for phylogenetic biogeographic analysis (Fortey and Cocks 1992; Lieberman 1997, 2000). After geographic distributions were placed at the tips of the tree, they were optimized to the ancestral nodes using a modified version of the Fitch (1971) parsimony algorithm described by Lieberman and Eldredge (1996) and

Lieberman (2000). The Fitch algorithm, in this context, assumes unordered transformations between areas. The area cladogram is shown in Figure 4.

Results

Phylogenetic biogeography provides two related types of information: First, the ranges of ancestral nodes are reconstructed permitting discussion of which areas were inhabited the ancestors of species or clades. Second, the mode of speciation (vicariance or dispersal) can be inferred for some cladogenetic events.

Examination of this area cladogram shows that the *L. (Leiopteria)* species included in this analysis are present ancestrally in the both the Appalachian and Michigan basins. Throughout most of the

evolutionary history of this group, speciation events were related to dispersal events that originated from the northern Appalachian basin. It is only relatively late in the phylogenetic history of this clade (near the terminus of the *L. (Leiopteria) auriculata* through *L. (Leiopteria) cornelli* clade), that the Southern Appalachian basin also became a center for evolution. Species inhabiting additional basins entered these regions by subsequent range expansions, which may correspond to episodes of traditional dispersal (sensu Humphries and Parenti 1986) or geodispersal (sensu Lieberman and Eldredge 1996). Episodes of range expansion seem frequent and can be identified by an expansion or shift in the geographic distribution of a descendant relative to its ancestor (indicated in Figure 4). By contrast, another prominent biogeographic pattern within these species is the limited amount of vicariant differentiation, which can be identified by a contraction in the range of a descendant species relative to its ancestor (indicated in Figure 4). In fact, there is evidence for only two episodes of vicariance in the history of this clade, and both of these occurred early in the history of the clade, at the first cladogenetic event recorded within the ingroup.

Implications

The paucity of vicariance seems low compared to documented levels of vicariant speciation in extant taxa described by Brooks and McLennan (1991). Reduction in speciation and increased dispersal in Middle to Late Devonian bivalves has been noted by Bailey (1978, 1983), who documented increased dispersal between

Europe and the Appalachian Basin in other bivalve lineages during the Middle Devonian, as well as reduced vicariant speciation in the Middle Devonian of Europe compared to the Early Devonian, and Amler (1999), who observed low speciation levels in Late Devonian European bivalve faunas. Lieberman (1999) also commented on the increased tendency for Middle Devonian trilobite taxa to disperse relative to Cambrian taxa. This was associated with a concomitant relative decline in vicariance. A relative reduction in vicariance with respect to dispersal was also observed in Middle and Late Devonian phyllocarids (Rode and Lieberman 2002). This relative lack of vicariance during the Middle to Late Devonian may be a cross-faunal phenomenon, and if so should be examined within the context of the dramatic biotic changes during the Middle and Late Devonian.

The Devonian was a time of intense biotic overturn that included a dramatic change from endemic Middle Devonian faunas to a cosmopolitan fauna during the Late Devonian (Boucot 1975; Oliver 1976, 1990; Bailey 1978, 1983; Klapper and Johnson 1980; McGhee 1981, 1996). The formation of this cosmopolitan biota can be attributed largely to sea level rise and the reduction of tectonic barriers to inter-basinal faunal exchange (Bailey 1978, 1983; McGhee 1996). These conditions would likely promote a decline in isolation of populations and hence vicariant speciation (Mayr 1942). Speciation rates can decline simply as a by-product of diminished opportunities for vicariance, and any clade that shows an extensive history of dispersal, along with minimal

vicariance, should show a tendency towards lowered speciation rates (Rode and Lieberman 2002).

Systematic Paleontology

SUBCLASS Pteriomorpha Beurlen 1944

ORDER Pterioidea Newell 1965

SUPERFAMILY Pterioidea Gray 1847

FAMILY Pterineidae Miller 1877

GENUS *Leptodesma* (*Leiopteria*) Hall 1883

Type species. *Leiopteria dekayi* Hall 1883, by subsequent designation (Miller 1889).

Discussion. *Leptodesma* (*Leiopteria*) was originally afforded a generic ranking by Hall (1883), but was transferred to *Leptodesma* as a subgenus by Newell and La Rocque (1969). Thus, *Leptodesma* (sensu Newell and La Rocque 1969) includes *L. (Leptodesma)* and *L. (Leiopteria)* Hall 1883, and these two subgenera are interpreted as sister taxa. Newell and La Rocque (1969) distinguished the subgenera based on the shape of the anterior auricle: rounded in *L. (Leiopteria)* and nasuate in *L. (Leptodesma)*. Additional characters that have been proposed to separate the taxa include a more oblique shape, smaller size, and less pronounced byssal sinus in *L. (Leptodesma)* (Williams and Breger 1916; Pojeta and others 1986). Another character, which is likely a synapomorphy for *L. (Leiopteria)*, is the presence of an anterior clavicle or septum (Williams and Breger 1916; Bradshaw 1999). The monophyly of *L. (Leiopteria)* is supported based on the stability of the previously proposed characters as observed in the specimens examined. Based on previous comments regarding the

phylogenetic validity of the two taxa (see Pojeta and others 1986; Amler 1995), additional analyses designed to examine the monophyly of *L. (Leiopteria)* would be worthwhile.

LEPTODESMA (LEIOPTERIA) ACCRANUS

RODE, NEW SPECIES

Figure 6.4.

Leiopteria sp.: Saul in Saul and others 1963:1045, pl. 136, figs. 18–19.

Types. The holotype is YPM 22385 (Figure 6.4), a left valve collected from the clay shale unit of the Accraian series of Early to Middle Devonian age. The specimen was collected in a small quarry (now covered over) on the coast just east of the Ambassador Hotel Beach and just west of Black Star Square in Accra, Ghana (Saul and others 1963).

Diagnosis. Shell small (holotype height 16.2 mm), greatest width along hingeline, posterior umbonal angle large, obliquity high, convexity moderate; anterior auricle large (approximately one-fourth of hingeline) with septum separating auricle from main body, byssal sinus weakly impressed; posterior wing small (approximately one-half of hingeline), embayment weak, wing tip not greatly extended, posterior wing weakly separated from main body; prominent, sharp comarginal lamellae constant on shell, forming distinct rows; lamellae group into sets of one prominent ring with several reduced rings.

Description. Small *L. (Leiopteria)* with subequal width and height. Angle of obliquity large (approximately 25°) result-

ing in a moderately recumbent posture. hingeline long relative to maximum length (approximately 90%). Ligament and lateral teeth not preserved. Anterior auricle large and rounded, separated from main body by septum. Anterior margin undulated with weakly impressed byssal notch. Posterior wing short. Separation of posterior wing from main body marked by inflection in ornamentation, but only weak change in convexity. Embayment of posterior wing apparent but not deep. Comarginal ornamentation well developed throughout entire shell. Growth bands are distinct ridges, but not all of same relief or prominence. On main shell body, prominent rings occur regularly separated by one or two less prominent rings. On anterior and posterior wings, ridges are subequal. No evidence of radial ornamentation or internal musculature observed.

Discussion. *Leptodesma* (*Leiopteria*) *acranus* is distinguished from other species of *L.* (*Leiopteria*) by the combination of a large anterior auricle, reduced posterior wing and embayment, and interspersed prominent and less prominent growth bands. This species is most closely related to *L.* (*Leiopteria*) *acutularis* and *L.* (*Leiopteria*) *cornelli*. All three species share the synapomorphies of growth lamellae that are both sharp and prominent in relief. *L.* (*Leiopteria*) *acutularis* and *L.* (*Leiopteria*) *cornelli* are distinguished by their maximum shell width located lateral to the hingeline.

Saul and others (1963) figured the holotype, but left the species in open nomenclature although they cited a positive identification to *L.* (*Leiopteria*). The

reconstructed phylogenetic position of this taxon as a distinct lineage within a well-resolved clade (Figures 2 and 3) indicates that a new species designation is appropriate.

Etymology. Named to reflect both Accra, Ghana, the collection locality, and the stratigraphic unit, the Accraian Series.

Other material examined. YPM 22386 (paratype).

Occurrence. Lower to Middle Devonian Accraian Series in Accra, along the Atlantic coast of Ghana.

LEPTODESMA (*LEIOPTERIA*) *ACUTULARIS*
POHL 1929

Figure 6.5.

Leiopteria acutularis; Pohl 1929:40–41, pl. 5, figs. 9–12.

Types. When Pohl (1929) originally described this species, he did not designate a holotype, and a lectotype has not been subsequently assigned. Therefore, MPM 13740 is designated herein as the lectotype. MPM 13740 is a left valve with excellent preservation of the anterior auricle and comarginal ornamentation. The shell is entire with the exception of the posterior wing.

Emended diagnosis. Shell small (height up to 14.0 mm), hingeline short, greatest width lateral to hingeline, posterior umbonal angle large, obliquity high, convexity high; anterior auricle large (approximately one-third of hingeline) with septum separating auricle from main body, byssal sinus

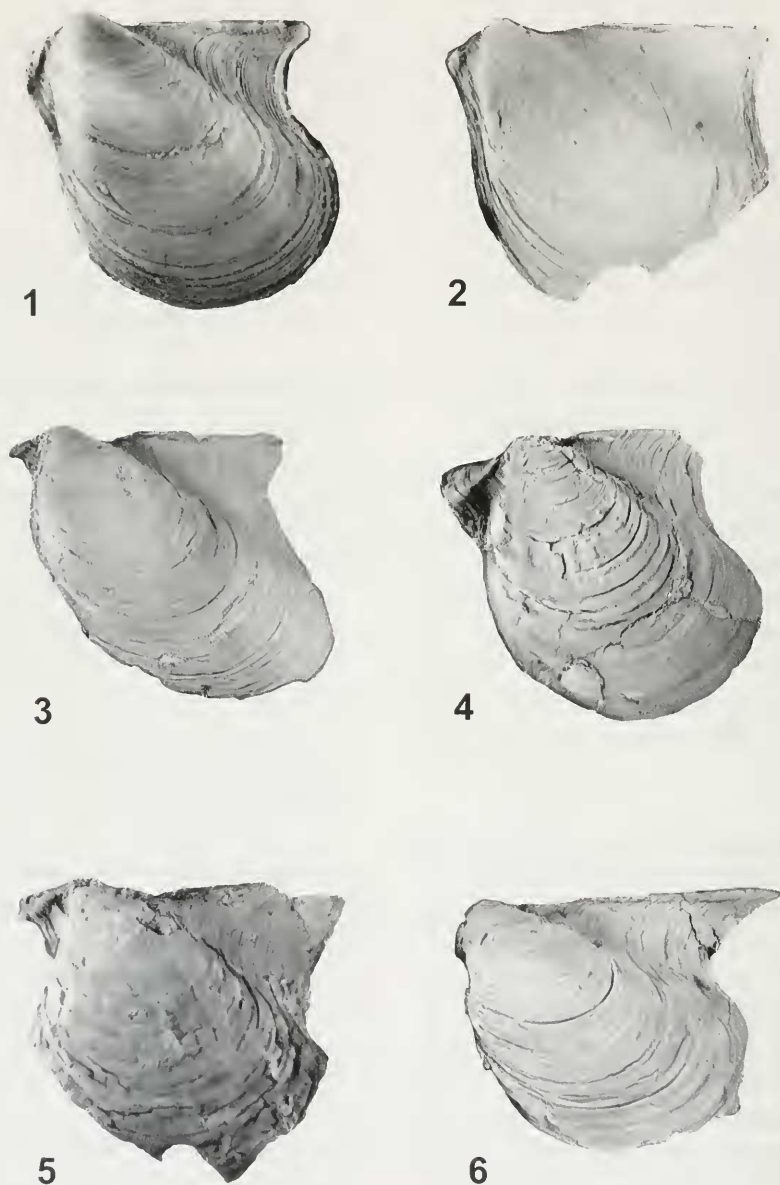


Figure 5

1, *Leptodesma (Leiopteria) ausablensis*, UMMP 38114 (holotype), left valve, 1.6 \times ; 2, *L. (Leiopteria) bigsbyi*, AMNH 5263 (lectotype), left valve, 1.4 \times ; 3, *L. (Leiopteria) nitida*, YPM 82914, left valve, 1.5 \times ; 4, *L. (Leiopteria) laevis*, left valve, 4.0 \times , AMNH 41903 (lectotype); 5, *L. (Leiopteria) laevis*, UMMP 24579 (formerly *L. (Leiopteria) peninsularis* [holotype]), left valve, 1.1 \times ; 6, *L. (Leiopteria) laevis*, AMNH 5264 (formerly *L. (Leiopteria) conradi* [syntype]), left valve, 1.1 \times .

strongly impressed; posterior wing small (approximately one-half of hingeline), posterior wing strongly separated from main body; prominent, sharp, crenulated comarginal lamellae constant on shell, forming distinct rows.

Other material examined. MPM 13739 (paralectotype).

Occurrence. Middle Devonian, Milwaukee Formation (Zone C), Milwaukee Co., Wisconsin.

LEPTODESMA (LEIOPTERIA) BIGSBYI
HALL 1883

Figure 5.2.

Leiopteria bigsbyi; Hall 1883:pl. 20, figs. 3, 11, 13–15; Hall 1884b:165–166, pl. 20, figs. 3, 11, 13–15, pl. 88, fig. 23; Clarke and Schwartz 1913:634–635, pl. 62, figs. 10–11; McAlester 1962:29.

Liopteria bigsbyi Hall; Miller 1889:484.

Types. Hall (1883) did not designate a holotype in the original description, and a lectotype has not subsequently been designated. Therefore, AMNH 5263 is herein designated as the lectotype. AMNH 5623 is a left valve with entire anterior and posterior extremities, as well as ornamentation preserved; part of the posterolateral margin is not preserved (Figure 6.1).

Emended diagnosis. Shell size medium (height 25 to 49 mm), hingeline long, posterior umbonal angle large, obliquity high, convexity high, umbo prominent; anterior auricle small (approximately one-fifth of hingeline); posterior wing large (approximately three-fourths of

hingeline), embayment weak, wing tip not greatly extended; prominent, dull comarginal lamellae constant on shell, forming distinct rows.

Other material examined. NYSM 2629–2632 (paralectotypes).

Occurrence. Middle Devonian, Hamilton Group, Pratts Falls, Onondaga Co., and Schoharie, Schoharie Co., New York.

LEPTODESMA (LEIOPTERIA) DEKAYI
HALL 1883

Figure 6.2.

Leiopteria dekayi; Hall 1883:pl. 19, fig. 1, pl. 20, figs. 16–18 (19 in error); Hall 1884b:164–165, pl. 19, fig. 1, pl. 20, figs. 16–18, pl. 88, figs. 5–10; Shimer and Schrock 1944:385, pl. 149, fig. 5; Ehlers and Wright 1959:10, pl. 1, figs. 3–4; McAlester 1962:29–31; Pojeta and others 1986:94–95, fig. 16a–16d.

Liopteria dekayi Hall; Miller 1889:484, fig. 835.

Leptodesma (Leiopteria) dekayi Hall; Newell and La Rocque 1969:N301, fig. C35, 6.

Types. Hall (1883) did not designate a holotype in the original description, and a lectotype has not subsequently been designated. Several previously illustrated specimens have limitations as a potential lectotype. NYSM 2639 is well preserved, but it was figured by Hall (1883:pl. 19, fig. 1, 1884b: pl. 19, fig. 1) with a radial ornament, which is lacking in this species. NYSM 2640 was illustrated by both Shimer and Shrock (1944) and Ehlers and Wright (1959), but this specimen was

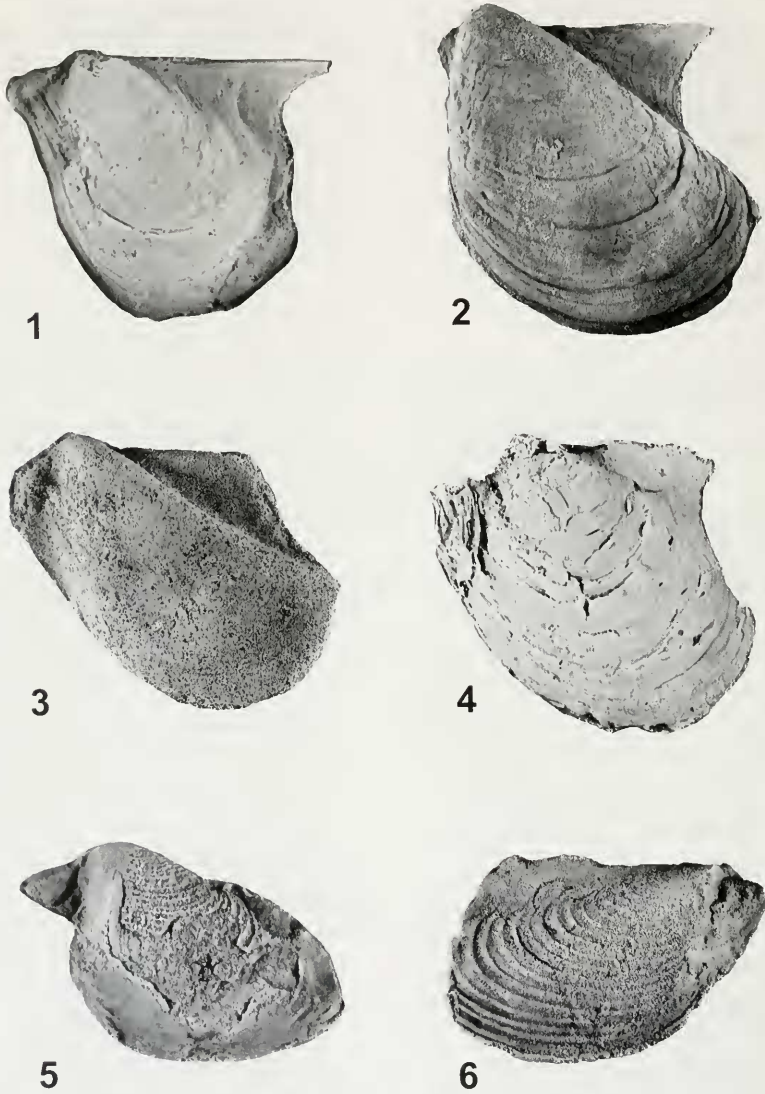


Figure 6

1, *Leptodesma (Leiopteria) leai*, NYSM 2658 (lectotype), left valve, 2.8 \times ; 2, *L. (Leiopteria) dekayi*, NYSM 2641 (lectotype), left valve, 1.8 \times ; 3, *L. (Leiopteria) torreyi*, NYSM 2671 (lectotype), left valve, 1.5 \times ; 4, *L. (Leiopteria) accrauus*, YPM 22385 (holotype), left valve, 3.3 \times ; 5, *L. (Leiopteria) acutilaris*, MPM 13740 (lectotype), left valve, 3.7 \times ; 6, *L. (Leiopteria) cornelli*, PRI 5242 (holotype), right valve, 1.3 \times .

collected from drift and hence has reduced stratigraphic control. It would be advantageous to choose the specimen figured in the Treatise (Newell and La Rocque 1969) for the lectotype specimen. However, this specimen is not a member of the syntype series and, therefore, ineligible for lectotype designation.

On the other hand, NYSM 2641 is a well-preserved left valve, with a complete anterior auricle that has the prominent anterior septum, an almost entirely preserved posterior wing, and well-developed ornamentation (Figure 6.2). NYSM 2641 has been previously illustrated as an exemplar of the species (Hall 1884b:pl. 20, fig. 17; Pojeta and others 1986), and is thus an appropriate choice for the lectotype; it is hereby so designated.

Emended diagnosis. Shell size medium (height range 19 to 36 mm), hingeline long, greatest width lateral to hingeline, posterior umbonal angle large, obliquity low, convexity high, umbo prominent; anterior auricle small (approximately one-fifth of hingeline), septum separating auricle from main body, byssal sinus weakly impressed; posterior wing large (approximately seven-tenths of hingeline), embayment pronounced, wing tip greatly extended, posterior wing strongly separated from main body; prominent, sharp comarginal lamellae constant on shell, forming distinct rows that increase in width posteriorly.

Other material examined. NYSM 2639–2640 and 2642 (paralectotypes), 2643–2647 (hypotypes), E1088–E1089.

Occurrence. Middle Devonian, Hamilton Group, Lake Skaneateles and Lake

Cayuga, Pratts Falls, Onondaga Co., Schoharie, Schoharie Co., New York.

LEPTODESMA (LEIOPTERIA) LAEVIS

HALL 1843

Figures 5.4, 5.5 and 5.6.

Leiopteria laevis; Hall 1843:181; Miller 1877:202; Hall 1883:pl. 17, figs. 5–11; Hall 1884b:158–159, pl. 17, figs. 5–11, pl. 20, fig. 5; Kindle in Prosser and Kindle 1913:253–254, pl. 29, fig. 6; Shimer and Schrock 1944:385, pl. 149, figs. 2–3.

Leiopteria laevis Hall; Miller 1889:484.

Leiopteria conradi; Hall 1883:pl. 20, figs. 1, 2, 4 (5 in error); Hall 1884b:159–160, pl. 20, figs. 1, 2, 4, pl. 88, figs. 1–4.

Leiopteria cf. *conradi* Hall; Kindle in Prosser and Kindle 1913:252–253, pl. 28, fig. 13.

Leiopteria couradi Hall; Miller 1889:484.

Leiopteria greenii; Hall 1883:pl. 20, figs. 9, 12; Hall 1884b:160, pl. 20, figs. 9, 12, pl. 88, figs. 21–22.

Leiopteria greenii Hall; Miller 1889:484.

Leiopteria mitchelli; Hall 1883:pl. 20, fig. 8; Hall 1884b:166–167, pl. 20, fig. 8, pl. 88, fig. 26; McAlester 1962:29.

Leiopteria mitchelli Hall; Miller 1889:484.

Leiopteria peninsularis; La Rocque 1950:283–284, pl. 4, figs. 1–2.

Leiopteria rafinesquii; Hall 1883:pl. 15, fig. 11, pl. 20, fig. 6–7; Hall 1884b:161–162, pl. 15, fig. 11, pl. 20, figs. 6–7, pl. 88, figs. 27–28; Walcott 1884:166, pl. 5, figs. 10, 10a; Shimer and Schrock 1944:385 pl. 149, fig. 5; Ehlers and Wright 1959:6–7, pl. 1, figs. 1–2.

Leiopteria rafinesquii Hall; Miller 1889:484, fig. 836.

Leiopteria sayi; Hall 1884b:162–163, pl.

88, figs. 15–20; McAlester 1962:29.

Leiopteria sayi Hall; Miller 1889:484.

Types. Hall (1843) did not designate a holotype in the original description, and a lectotype has not subsequently been designated. AMNH 41903 is here designated as the lectotype. AMNH 41903 is a well-preserved entire left valve (Figure 5.4). The anterior auricle and posterior wings are preserved in detail, as is the comarginal ornamentation. This specimen was figured previously by Hall (1883:pl. 17, fig. 10, 1884b:pl. 17, fig. 10).

Emended diagnosis. Shell small to large, body obliquely ovate, hingeline long, convexity low, posterior umbonal angle large, umbo pronounced; anterior auricle small, septum present; posterior wing with pronounced embayment, often extended into acuminate projection, typically demarcated from body by distinct groove; sharp growth bands developed constantly over shell, width may increase posteriorly; lamellose growth bands apparent in larger specimens.

Discussion. The oversplitting of *L. (Leiopteria)* species of Hall (1883, 1884b) has long been recognized (Williams and Breger 1913; Rau 1955; McAlester 1962). The original species designations were often based on only a few specimens and frequently only from a single locality (for example, *L. (Leiopteria) mitchelli* and *L. (Leiopteria) greeni*). *Leptodesma (Leiopteria) laevis*, *L. (Leiopteria) conradi*, *L. (Leiopteria) greeni*, *L. (Leiopteria) mitchelli* and *L. (Leiopteria) sayi* are known only from dark shale facies of the Middle Devonian Hamilton Group of

New York. Of the two additional species, *L. (Leiopteria) peninsularis* is known only from the Middle Devonian Dundee Limestone of Michigan, while *L. (Leiopteria) rafinesquii* has been recorded from the Hamilton Group of New York and the Delaware Limestone of central Ohio and Early Devonian strata of Nevada. The lack of resolution within the phylogenetic analysis suggests that the other six species are not well established and morphological characters (at least those included within this analysis) do not distinguish them from *L. (Leiopteria) laevis*.

The morphologies of the six newly synonymized species are indistinguishable. However, smaller specimens (those formerly referred to *L. (Leiopteria) laevis* under Hall's description [1884b]) tend to have comarginal ornamentation of distinct, sharp bands (Figure 5.4). Larger specimens, however, all have lamellose ornamentation in which each growth band is a platform rather than a narrow raised ridge (Figure 5.5 and 5.6). Additionally, a gradation of relative amount of posterior wing projection can be observed within the revised species. In general, as size increases, the relative amount of projection increases (compare Figure 5.4 and 5.6). More examples of such gradations may exist and further analysis could place such changes within an ontogenetic or environmental context.

Other material examined. *Leptodesma (Leiopteria) laevis* Hall: AMNH 41903–41904 (syntypes), NYSM 2652–2657 (hypotypes); *L. (Leiopteria) conradi* Hall: AMNH 5264 (syntype), NYSM 2634–2635 (syntypes), 2636–2638 (hypotypes); *L. (Leiopteria) greeni* Hall:

AMNH 5265 (syntype), NYSM 2649 (syntype), 2650–2651 (hypotypes); *L. (Leiopteria) mitchelli* Hall: AMNH 5266 (holotype); *L. (Leiopteria) peninsularis* La Rocque: UMMP 24579 (holotype), 24580 (paratype); *L. (Leiopteria) rafinesquii* Hall: NYSM 2663 (lectotype), 2661–2662 and 2664 (paratypes), AMNH 4208 (hypotype), USNM 13882 (6 specimens); *L. (Leiopteria) sayi* Hall: NYSM 2665–2670 (syntypes).

Occurrence. Lower Devonian of the Eureka District, Nevada. Delaware Limestone, Delaware, Ohio. Marcellus Shale at Littleville, Livingston Co., Alden, Erie Co., and East Bloomfield, Ontario Co., New York. Hamilton Shales at Lake Cayuga, Lake Skaneateles and Lake Canandaigua; Bellona, Yates Co., Leonardsville, Madison Co., Norton's Landing, Cayuga Co., and Ontario Co., New York. Coarse grits in Schoharie Co., New York. Romney Formation, Onondaga Member, near Old Town and Cumberland, Maryland.

LEPTODESMA (LEIOPTERIA) LEAI

HALL 1884

Figure 6.1.

Leiopteria leai; Hall 1884b:168–169. pl. 88, figs. 24–25; McAlester 1962:29.

Liopteria leai Hall; Miller 1889:484.

Types. Hall (1884b) did not designate a holotype in the original description, and a lectotype has not subsequently been designated. Therefore, NYSM 2658 is here designated as the lectotype. NYSM 2658 is a left valve in which the anterior auricle is entire. The tip of the posterior wing is absent and part of the posterolateral margin is not preserved (Figure 6.1). NYSM

2658 is a better choice for the lectotype than NYSM 2659 because the latter lacks in the anterior auricle, umbo and posterior wing tip (Hall 1884b:pl. 88, fig. 25).

Emended diagnosis. Shell small (height ranges from 14 to 23 mm), hingeline long, greatest width along hingeline, posterior umbonal angle large, obliquity high, convexity high, umbo moderate; anterior auricle large (approximately one-fourth of hingeline) with septum separating auricle from main body, byssal sinus weakly impressed; posterior wing large (up to three-fourths of hingeline), embayment pronounced, wing tip greatly extended, posterior wing strongly separated from main body; prominent, dull comarginal lamellae constant on shell, forming distinct rows.

Other material examined. NYSM 2659 (paralectotype).

Occurrence. Middle Devonian, Hamilton Group, southern Schoharie Co., New York.

LEPTODESMA (LEIOPTERIA) TORREYI

HALL 1884

Figure 6.3.

Leiopteria torreyi; Hall 1884b:174. pl. 22, figs. 6–7, pl. 88, fig. 11; McAlester 1962:29.

Liopteria torreyi Hall; Miller 1889:484.

Types. Hall (1884b) did not designate a holotype in the original description, and a lectotype has not subsequently been designated. Therefore, NYSM 2671 is here designated as the lectotype. NYSM 2671 is

a complete left valve in which the anterior auricle, posterior wing and ornamentation are all well preserved.

Emended diagnosis. Shell small (height ranges from 21 to 22 mm), hingeline short, greatest width along hingeline, posterior umbonal angle large, obliquity high, convexity high, umbo moderate; anterior auricle small (approximately one-sixth of hingeline) with septum separating auricle from main body, byssal sinus weakly impressed; posterior wing large (approximately five-sixths of hingeline), embayment weak, wing tip not greatly extended, posterior wing strongly separated from main body; dull comarginal lamellae constant on shell, forming distinct rows.

Other material examined. NYSM 2672 (paralectotype).

Occurrence. Late Devonian, Chemung Group, near Panama, New York.

Notes on Material Examined

The following taxa and material examined do not require synonymy, lectotype designation, or detailed discussion: *Leptodesma* (*Leiopteria*) *auriculata* Clarke and Schwartz 1913: USNM 178306 (holotype); *L.* (*Leiopteria*) *ausablensis* Ehlers and Wright 1959: UMMP 38114 (holotype), and 38111–38113, 38115–38119 (paratypes); *L.* (*Leiopteria*) *cornelli* Caster 1930: PRI 5242 (holotype); *L.* (*Leiopteria*) *gabbi* Hall 1884b: NYSM 2648 (holotype); *L.* (*Leiopteria*) *linguiformis* Hall 1884b: NYSM 8870 (holotype); *L.* (*Leiopteria*) *marylandica* Clarke and Schwartz 1913: USNM 178288–178289 (syntypes);

L. (*Leiopteria*) *nitida* Hall 1883: YPM 21378, 21380, 21382, 21384A, 22655–22656, 82914, NYSM 2633 (holotype); *L.* (*Leiopteria*) *oweni* Hall 1883: NYSM 2660 (holotype); *L.* (*Leiopteria*) *troosti* Hall 1884b: NYSM 2673 (holotype); *L.* (*Leptodesma*) *spinerigum* (Conrad 1842) [type lost]: YPM 21414, 21450 (hypotypes), AMNH 6094 (hypotype).

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